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A COMPARATIVE REVIEW OF THE SPAWNING, DEVELOPMENT AND METAMORPHOSIS OF PROSOBRANCH AND OPISTHOBRANCH GASTROPODS WITH SPECIAL REFERENCE TO THOSE FROM THE NORTHWESTERN RED SEA

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ABSTRACT

Aspects of spawning, development and metamorphosis of 50 prosobranch and opisthobranch gastropods from the northwestern Red Sea are reviewed. For almost every species, data are given of the breeding season, size and number of eggs laid, and period and type of development. The early embryology, larval structure and behaviour, and post-larval development are summarized. Only the nudibranch *Casella obsoleta* has direct development. In agreement with Thorson's rule, most species have pelagic development, although prosobranchs (neogastropods in particular) show a tendency towards lecithotrophy and rapid metamorphosis. The intrinsic and extrinsic factors affecting the type of development are discussed.

INTRODUCTION

In an attempt to review reproduction in prosobranchs and opisthobranchs, a study of their egg masses has recently been made (Soliman, 1987). The present paper aims to extend the comparative study to other aspects of reproduction, namely egg size and number, early embryology, larval structure and behaviour, and the type of reproduction, and to review the factors which affect development and metamorphosis. This paper also aims to find out to what extent the patterns of molluscan development in the northwestern Red Sea agree with Thorson's rule (1950) and to compare our results with those reported from other areas lying more or less within the same latitudes.

The present study, like the former, is based mainly on new data and on studies made on Red Sea gastropods during the last 30 years (Gohar & Aboul-Ela, 1957, 1959; Gohar & Eisawy, 1963,1967; Gohar & Soliman, 1963, 1967; Eisawy & Sorial, 1968, 1974, 1976; Eisawy, 1970; Soliman, 1977, 1978, 1980, 1983, 1986) together with data from other sources.

SPAWNING, EMBRYOLOGY AND LARVAL DEVELOPMENT

Egg Capsules

Primitively, gastropod eggs are laid singly, uncovered and they are externally fertilized. In most gastropods, however, eggs are enclosed either singly or in groups (up to hundreds) in transparent thin-walled cases, in leathery sacs or hard capsules. Cases may be dispersed freely becoming planktonic. Most often they are embedded in a gelatinous matrix and moulded in thin sheets, ovoid or globular jelly masses (or without a definite shape), cords or ribbons (Soliman, 1987).

In opisthobranchs, egg cases may lie directly in the spawn jelly or, as in many nudibranch egg ribbons, may be primarily enclosed in tubes of thick mucus winding in the spawn matrix in variable fashion. Thus in small ribbons the tubes run in a closely parallel manner (Fig. 1A), but they radiate peripherally in massive undulating ones (Fig. 1B). In some species, each egg case within the tube may be isolated in a thin-walled compartment of various shapes (Fig. 1C,D). The egg string of *Strombus tricornis* (Eisawy & Sorial, 1968) has a similar construction with the egg cases each enclosed in a gelatinous compartment that is finally coated by the egg string (Fig. 1E).

The size limits of opisthobranch egg cases (and the numbers of eggs enclosed) are generally lower than those recorded for prosobranch capsules (Table 1). In the former, cases measure 0.1–0.3 mm on average, but cases up to 0.6 mm across are not uncommon. The largest cases encountered in some masses of the nudibranch *Hexabranchus sanguineus* (2 x 0.6 mm, with more than 100 eggs) (Gohar & Soliman, 1963b) are still far smaller than what exists in certain proso-

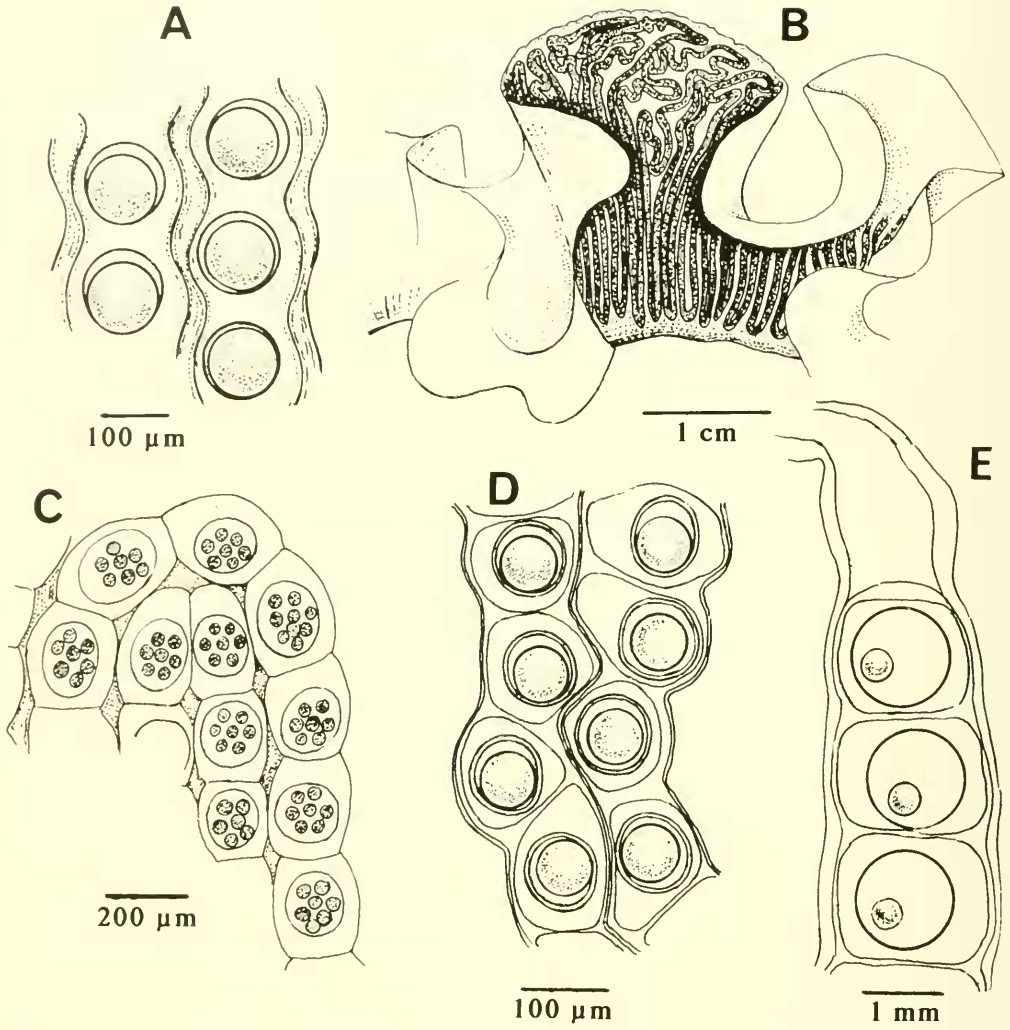


FIG. 1. Patterns of egg case arrangement in the jelly matrix in Red Sea gastropods. A. *Trippa spongiosa:* part of two parallel egg cords in jelly with no compartments (after Gohar & Soliman, 1967g). B. *Discodoris concinna:* enlarged portion of spawn ribbon with cords radiating and winding distally (modified after Gohar & Soliman, 1967f). C. *Asteronotus cespitosus:* segmented egg cord with one case in each segment (after Gohar & Soliman, 1967e). D. *Chromodoris inornata:* egg cases with each enclosed in a separate compartment (after Gohar & Soliman, 1967b). E. *Strombus tricornis:* similar arrangement to D, but eggs are in cords, not in a common jelly (after Eisawy & Sorial, 1968).

branchs (19–35 x 5–9 mm in *Pleuroploca trapezium* with up to 400 eggs, and 8–9 x 3.5 mm in *Nassa francolina* with up to 1678 eggs) (Gohar & Eisawy, 1967b).

Size and number of eggs

The number of eggs laid by a gastropod is inversely proportional to egg size. According to the available data, the maximal size attained in prosobranchs markedly exceeds that in opisthobranchs (up to 0.75 mm in *Conus* (Natarajan, 1957), 0.44 mm in *Strombus tricornis* (Eisawy & Sorial, 1968) and 0.42 mm in *Pleuroploca trapezium* (Gohar & Eisawy, 1967b), against only 0.39 mm in *Cadlina laevis* (Thompson, 1967) and 0.33 mm in *Casella obsoleta* (Gohar & Soliman, 1967d)). As

anticipated, the number of eggs in a spawn deposited by an opisthobranch substantially surpasses what is recorded for prosobranchs (apart from certain archaeogastropods). 148 million eggs were recorded laid by *Aplysia californica* (MacGinitie, 1934) and a little less than 5 million by the nudibranch *Asteronotus cespitosus* (Gohar & Soliman, 1967e).

However, in many prosobranchs (principally neogastropods) the majority of eggs laid act as nurse cells subserving as food for the very small fraction of viable eggs which proceed to full development (15% in *Pleuroploca trapezium*, < 6% in *Chicoreus ramosus* (Gohar & Eisawy, 1967b), 3% in *Fusinus tuberculata* (Eisawy & Sorial, 1976a), 2% in *Chicoreus virgineus* (Gohar & Eisawy, 1967b), and even less in certain other species). According to Thorson (1940) 50,000–100,000 nurse eggs may exist per embryo in *Volutopsius norwegicus*. Nurse cells are not reported to exist in opisthobranchs.

Cleavage and early embryology

In the majority of opisthobranchs, the two initial divisions of the egg invariably bring about the formation of nearly equal macromeres which proceed thereafter in typical spiral cleavage (Fig. 2A). Unequal division is, however, typical of large, yolky prosobranch eggs. Actually such division is mainly dependent on the amount of yolk in the egg irrespective of its size. Thus while the initial division of *Tonna olearium* eggs (0.25 mm in diameter) gives rise to nearly equal macromeres (Gohar & Eisawy, 1967a), similar or even smaller eggs of other species (0.18–0.22 mm, *Chicoreus virgineus;* 0.25 mm, *C. ramosus* (Gohar & Eisawy, 1967b)) exhibit markedly unequal division with the macromeres A-C appearing as if budding from the giant D cell (Fig. 2B). The subsequent divisions do not much affect the relative disparity in the size of the macromeres.

In contrast to the opacity of most gastropod embryos and larvae developing from lecithotrophic eggs, planktonic larvae are relatively transparent. It is not uncommon nevertheless to come across opaque embryos arising from comparatively small eggs (70 μm, *Sebadoris crosslandi* (Soliman, 1980)) or, conversely, lecithotrophic larvae (*Trippa spongiosa*, egg 0.2 mm across (Gohar & Soliman, 1967g)) or veliger and metamorphosing stages of directly developed species (*Acteocina atrata* (Mikkelsen & Mikkelsen, 1984)) with markedly clear structure. Generally, however, as far as the planktotrophic Red Sea gastropods are concerned, the developmental stages of opisthobranchs are much more transparent than are those of prosobranchs. Particularly in *Hexabranchus sanguineus* (Gohar & Soliman, 1963b), with intensely red yolk globules mostly condensed at the vegetative side of the egg, it is possible to follow, in whole live embryos, the formation of the 4d mesoblast and its division into two cells (Fig. 2C), which remain visible even after their migration inwards between the future ectoderm and endoderm. In fact, *H. sanguineus,* because of its abundance, the huge number of eggs it lays, and the clarity of its cells, is ideal material for live study of spiral cleavage, cell lineage and germ layer formation in molluscs.

Among the structures to appear early in opisthobranch embryos are the anal cells. These are initially posteroventral and slightly to the left. Their gradual shifting to the anterior right side (with the future proctodeal invagination and anus) is the only ontogenetic evidence of torsion, which is thus much less than 180°. *Casella obsoleta* exhibits detorsion (Fig. 5D) (Gohar & Soliman, 1967d), with the anal cells and associated organs migrating posteriorly (with the hind gut) during metamorphosis, until they reach their final position in the middle line just in front of the secondary larval kidney. They persist for 7–10 days after hatching and eventually vanish. This differs from Bonar's (1976) report that the anal cells disappear by the time the secondary kidneys develop.

The mouth in some cases forms shortly before the complete closure of the blastopore. In a number of species (*Dendrodoris fumata* (Fig. 4A), *Chromodoris inornata*) the secondary larval kidney develops as early as the anal cells (Gohar & Soliman, 1967a,b). It attains its maximal development structurally and functionally during larval life. It is still encountered in the hatching juvenile of *Casella obsoleta,* but gradually diminishes in size and disappears in three weeks, i.e. after the disappearance of the anal cells.

Hatching and larval behaviour

At hatching, the whole upper wall of the neritid capsule detaches, thus liberating the larvae (Soliman, 1987). In neogastropods in particular (and certain mesogastropods, e.g. *Tonna olearium* (Gohar & Eisawy, 1967a)),

TABLE 1. Breeding season, size, number and type of development of eggs of Red Sea prosobranchs and opisthobranchs.

Species	Breeding season	Dimension(s) of egg-case or capsule (mm)	Number of eggs per case or capsule	Max. number of eggs deposited
PROSOBRANCHS				
Trochus erythraeus	May–Aug	0.124–0.15 x 0.148–0.17	1–2	11,200
Trochus dentatus	Apr–Jul	0.4,0.48 x 0.43 av.	1	—
Turbo radiatus	Feb–May	—	1	—
Nerita forskali	Jan–Oct	2.2–2.5	60–210	—
*Lambis truncata**	Apr–Jul	0.3	1	21,750
Strombus tricornis	May–Aug	1.2–1.3	1	2,800
Strombus gibberulus	—	—	1	—
Strombus fasciatus	—	—	1	157,000
*Polinices mammilla**	Aug–Sep	0.135	1	580,000
*Polinices melanostoma**	—	—	1	61,000
*Tonna olearium**	Aug–Sep	1.4–1.9 x 1–1.5	18–35	—
*Chicoreus virgineus**	Apr–Jul	12–20 x 10–12	1036–2511	625,000
*Chicoreus ramosus**	Apr–May	15–21 x 5–7	300–346	13,450
*Nassa francolina**	Jul–Dec	8–9 x 3.5	1390–1723	1,720
Thais savignyi	Aug–Nov	3.5–3.7 x 2.2–3	250–500	15,000
Leptoconchus cumingii	Feb–Nov	6–9 x 3.7–6.3	600–1600	—
Leptoconchus globosus	Feb–Nov	7–8 x 5–6	700–1800	11,250
Magilopsis lamarckii	Feb–Nov	5–7 x 3.5–4.5	500–1400	—
*Pleuroploca trapezium**	Apr–May	19–35 x 5–9	70–400	70,000
*Fusinus tuberculatus**	Feb–May	11 x 7	—	—
Conus sp.	—	—	—	—
Conus sp.	—	—	—	—
OPISTHOBRANCHS				
Aplysia dactylomela	Apr–Oct	—	4–7	>1,000,000
Dolabella auricularia	Apr–Oct	—	1	>5,000,000
Berthellina citrina	Annual	0.38–0.44	1	23,760
Phyllobranchillus orientalis	Jun–?	0.09	1	117,000
Elysia olivaceus	May–Aug	—	—	—
Nembrotha limaciformis	Jun–Aug	0.09 x 0.075	1	75,600
Gymnodoris sp.	Jun–Sep	0.19 x 0.22 av.	1	61,500
Hexabranchus sanguineus	Annual	0.3–0.7, 0.6–1 x 0.2–0.4 up to 2 x 0.6	4–30 100	4,063,500
Chromodoris quadricolor	Mar–Sep	0.1–0.135	1	68,400
Chromodoris pulchella	Mar–Apr	—	1	48,000
Chromodoris annulata	Jul–?	—	1	108,000
Chromodoris ghardaqana	—	—	1	—
Chromodoris inornata	May–Nov	0.1	1	161,000
Chromodoris tinctoria	Jun–Jul	0.15	1–2	62,000
Chromodoris pallida	Jun–?	—	—	—
Casella atromarginata	Jun–Aug	0.25	1	188,000
Casella obsoleta	May–Sep	0.52–0.58	1	1,900
Asteronotus cespitosus	May–Sep	0.18–0.24	7–10	4,885,650
Platydoris scabra	May–Sep	0.16 x 0.23	1	1,507,520
Discodoris erythraeensis	Feb–Sep	0.24–0.25	1	56,100
Discodoris concinna	May–Sep	0.11–0.126	1	3,796,700
Discodoris sp.	Jul–?	—	1	21,760
Trippa areolata	May–Nov	0.11	1	4,113,500
Trippa spongiosa	Jun–?	0.26–0.3	1	103,600
Sebadoris crosslandi	Jun–Jul	0.12	1	902,000
Dendrodoris fumata	Annual	0.11–0.135	1	165,000
Phyllidia varicosa	Jul–Oct	0.2	1	67,000
Phyllodesmium xeniae	May–Oct	0.13–0.14	1	11,200

*Nomenclature updated.

Egg diameter (μm)	Period to veliger formation (d)	Temperature of culture (°C)	Type of development[†]	Reference
75	3–4	28	P	Gohar & Eisawy, 1963
200–225	24 h	27.5	L	Eisawy, 1970
200	8–9	26	L	Eisawy & Sorial, 1974a
120	—	—	P	Pers. obs.
210–260	7	26	L	Gohar & Eisawy, 1967a
410–440	10–11	28	L	Eisawy & Sorial, 1968
90	3–4	28	P	Eisawy & Sorial, 1976b
130	—	—	P	Eisawy & Sorial, 1976b
—	8	—	P	Gohar & Eisawy, 1967a
—	—	—	P	Gohar & Eisawy, 1967a
240–250	25	25	L	Gohar & Eisawy, 1967a
180–200	40–45	26.5	L	Gohar & Eisawy, 1967b
250	35–38	25	L	Gohar & Eisawy, 1967b
180	30–32	20	P	Gohar & Eisawy, 1967b
185–190	30–60	28–21	L	Eisawy & Sorial, 1974b
200	—	—	P	Gohar & Soliman, 1963a
—	—	—	P	Gohar & Soliman, 1963a
—	—	—	P	Gohar & Soliman, 1963a
400–420	45–47	24	L	Gohar & Eisawy, 1967b
180–200	30–50	22–17	L	Eisawy & Sorial, 1976a
—	—	—	P	Gohar & Eisawy, 1967b
—	—	—	L	Gohar & Eisawy, 1967b
80	7–10	22–30	P	Pers. obs.
92	8–11	22–30	P	Pers. obs.
200–250	7	28.5	L	Gohar & Aboul-Ela, 1957a
60	7½	27	P	Pers. obs.
—	—	—	P	Pers. obs.
65	4½	28	P	Pers. obs.
140	8	26	P	Pers. obs.
110–120	6–12	30–16	P	Gohar & Soliman, 1963b
70–90	12	18	P	Gohar & Aboul-Ela, 1957c
120–170	6	20.5	P	Gohar & Aboul-Ela, 1957c
120–160	6½	29	P	Gohar & Aboul-Ela, 1957c
—	—	—	—	Gohar & Aboul-Ela, 1957c
80	7–9½	30–22	P	Gohar & Soliman, 1967b
100	6–6½	29–27.4	P	Gohar & Soliman, 1967c
—	—	—	P	Pers. obs.
130–140	10	25	P	Gohar & Aboul-Ela, 1959
300–330	13–14	25	D	Gohar & Soliman, 1967d
65–70	4–5½	27.8–24.8	P	Gohar & Soliman, 1967e
90–100	5–5½	27.6	P	Soliman, 1978
140	11½	19	L	Gohar & Aboul-Ela, 1959
75	4½	27.5	P	Gohar & Soliman, 1967f
93	7½	29	P	Pers. obs.
100	4–5¼	27.4–23.9	P	Gohar & Soliman, 1967g
200	7	27	L	Gohar & Soliman, 1967g
70	7	27.6	P	Soliman, 1980
100	5½–17	30–16	P	Gohar & Soliman, 1967a
100	10	27.5	P	Soliman, 1986
95	4	28.5	P	Gohar & Aboul-Ela, 1957b

[†]P, planktotrophic; L, lecithotrophic; D, direct development.

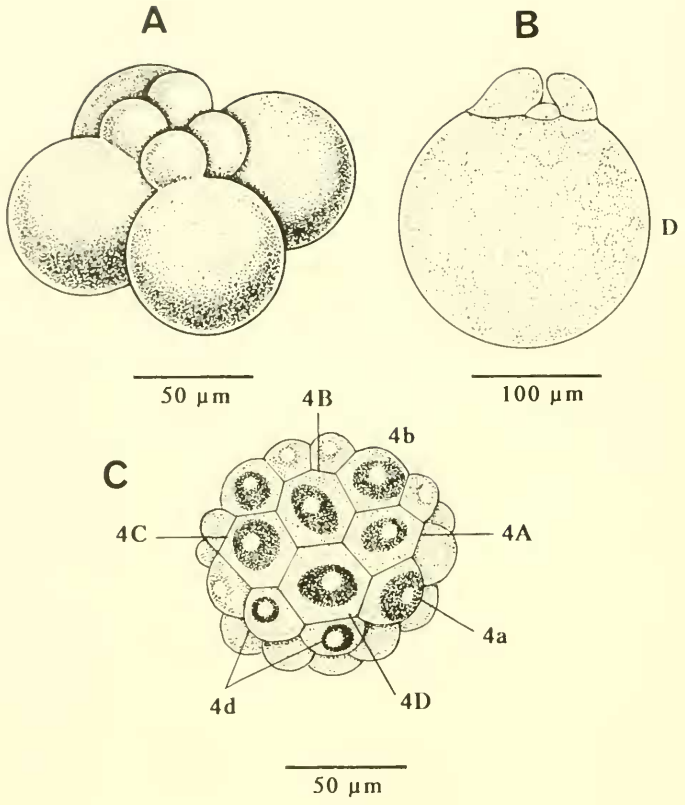


FIG. 2. Early embryology of Red Sea gastropods. A. *Hexabranchus sanguineus:* spiral cleavage, first quartette of micromeres formed (after Gohar & Soliman, 1963b). B. *Chicoreus virgineus:* unequal cleavage of egg in a lecithotrophic prosobranch (after Gohar & Eisawy, 1967b). C. *Hexabranchus sanguineus:* formation of mesoderm mother cell (the mesoblast 4d) (after Gohar & Soliman, 1963b).

the egg capsule has an exit hole with fixed shape and position. The exit hole remains closed throughout development but opens at hatching to permit the release of larvae or succeeding stages. Empty capsules remain intact with firm walls. No comparable exit holes are encountered in opisthobranchs. In the Red Sea opisthobranch species studied, as development proceeds, the embryonic capsules gradually increase in size becoming

turgid with extremely thin walls (apparently due to increased intracapsular osmotic pressure). This allows for an easy penetration by the hatching stages. In only a few cases did the perforated capsules retain their contour. Generally, however, they become collapsed, deformed or entirely ruptured and so can be barely detected in the jelly matrix. This latter in turn may either remain intact, become wrinkled, dissociate into fragments or be converted into thick mucus.

The wide temperature range (16–30°C) and high salinity (around 40‰) of Red Sea waters directly affect the development and larval behaviour of the gastropods studied. In species with extended breeding, the developmental time varies much with temperature (e.g. *Thais savignyi,* 30 d at 28°C, 38 d at 26°C and 45 d at 24.2°C (Eisawy & Sorial, 1974b); *Fusinus tuberculatus,* 30–32 d at 27°C and 45–50 d at 22°C (Eisawy & Sorial, 1976a); *Hexabranchus sanguineus*, 6 d at 27°C and 10 d at 23.5°C (Gohar & Soliman, 1963b); *Dendrodoris fumata,* 5½ d at 28°C and 17 d at 17°C (Gohar & Soliman, 1967a)). The latter species is interesting since the length of the developmental period varies with the slight thermal changes within the same month: 152 h at 26.2°C, 156 h at 25.6°C and 164 h at 25°C. Being a shore species subject to substantial fluctuations in temperature and salinity, its larvae display remarkable tolerance to salinity changes (surviving for several days in 30‰ and for 40 h in 50‰).

At hatching, planktotrophic larvae develop for some time marked positive phototaxis, pursuing phytoplankton for food, and negative geotaxis to effect larval dispersal. Thereafter they become positively geotactic, invariably moving near the bottom but without displaying any tendency to metamorphose for reasons discussed later. Lecithotrophic larvae may remain planktonic for days or hours; they eventually settle and metamorphose. The newly emerging juveniles of *Casella obsoleta,* like the adults, are nocturnal in habit (Gohar & Soliman, 1967d).

Light has a decisive effect on the degree of pigmentation of the veliger shell, and in turn on the general colour of the spawn mass. Even in the same ribbon of *D. fumata,* parts exposed to more light appear darker (Gohar & Soliman, 1967a). Light affects the whole process of development: in the total absence of light it has been shown experimentally that development is retarded or completely inhibited.

Larval Structure

The velum, foot and shell are among the most conspicuous gastropod larval organs which can be of outstanding taxonomic value in prosobranchs.

The enlargement and subdivision of the velum into 4, 6 or more lobes is a common character of large prosobranch larvae (of advanced mesogastropods and neogastropods) which helps them meet their needs for buoyancy and food (Fig. 3A). A large or subdivided velum is not an indication of a long planktonic existence as is sometimes stated (Gohar & Eisawy, 1967a, in the case of *Polinices melanostoma*). Many such larvae have only a short pelagic life, becoming benthic one or two days after hatching; the velar lobes are eventually resorbed (e.g. *Strombus tricornis* (Eisawy & Sorial, 1968), *Chicoreus ramosus* (Fig. 3B, C), *Pleuroploca trapezium* (Gohar & Eisawy, 1967b), *Fusinus tuberculata* (Eisawy & Sorial, 1976a)). A multilobed velum is reported to exist in the larvae of only one opisthobranch, *Philine denticulata* (Horikoshi, 1967). In lecithotrophic and directly-developing opisthobranchs in general, the velum is relatively reduced in size and mobility. During metamorphosis, it may take part in the formation of the juvenile rhinophores (*Casella obsoleta,* Gohar & Soliman, 1967d).

A pedal operculum does not form in directly-developing opisthobranchs. It is lost in early juvenile development in aplysiids (Switzer-Dunlap & Hadfield, 1977), or during metamorphosis in all other opisthobranchs, but in prosobranchs it is only lost in a few non-operculate species.

With only a few exceptions, the larval shell is dextral in prosobranchs, with 1½ to 3 whorls (*Chicoreus ramosus*, Gohar & Eisawy, 1967b). In opisthobranch larvae, it may be cup-shaped, inflated or incipiently sinistrally coiled (hyperstrophic) with ¾–1½ whorls. Anomalous larvae possessing large tubular uncoiled shells are commonly observed in those opisthobranchs laying millions of eggs (*H. sanguineus, Asteronotus cespitosus* (Gohar & Soliman, 1963b, 1967e), *Platydoris scabra* (Soliman, 1978)). While the larval shell is retained in shelled opisthobranchs, it is cast off during metamorphosis in the remaining opisthobranch groups.

Except for *Casella obsoleta* and *Phyllodesmium xeniae* (Gohar & Aboul-Ela, 1957b), the veliger shells of all other Red Sea opisthobranchs studied belong to type B of Vester-

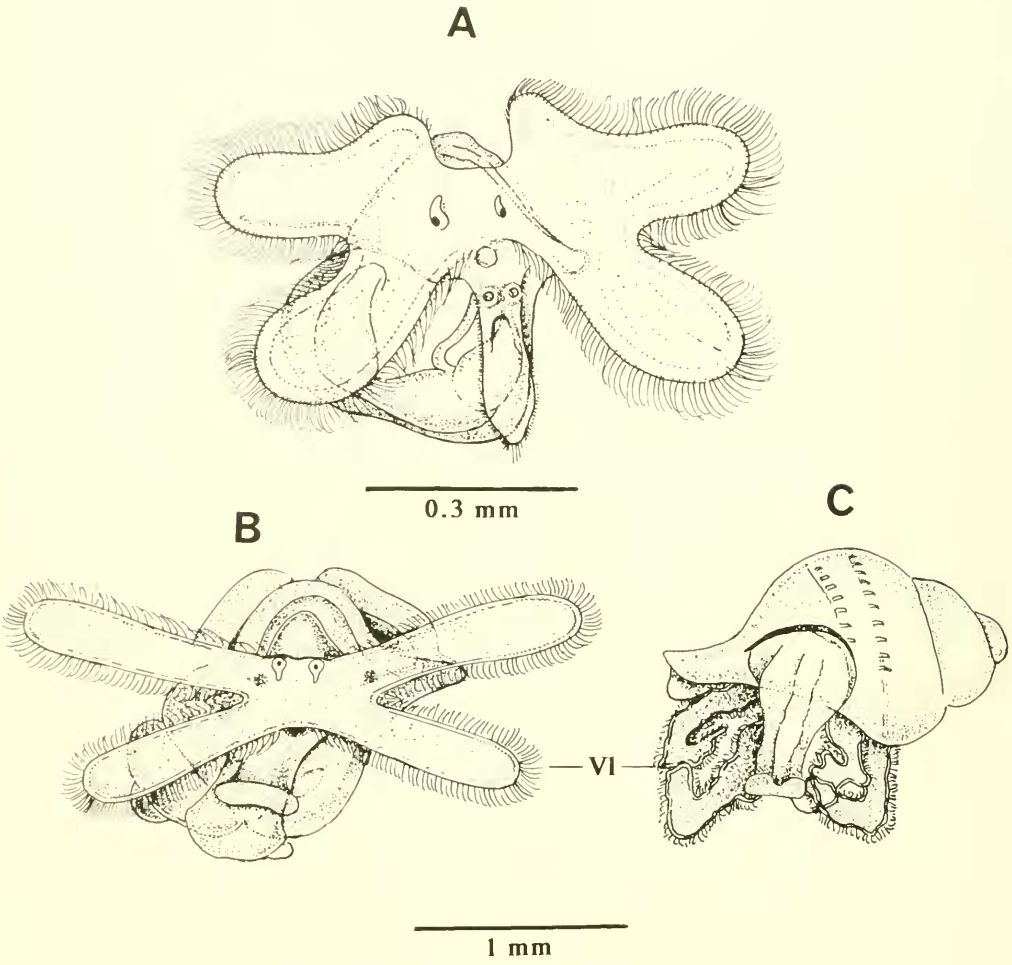


FIG. 3. Larval structure and development of Red Sea prosobranchs. A. *Lambis truncata:* veliger larva with 6-lobed velum (after Gohar & Eisawy, 1967a). B. *Chicoreus ramosus:* newly hatched veliger with 4-lobed velum (after Gohar & Eisawy, 1967b). C. *Chicoreus ramosus:* postlarva showing degeneration of velum during metamorphosis (after Gohar & Eisawy, 1967b). Vl, velum.

gaard & Thorson (1938) and Thorson (1946). While the larval shell type of *P. xeniae* was not reported, that of *C. obsoleta* is of type A. The validity of the latter type was a matter of controversy (Soliman, 1977). It has been rejected by Thompson (1961) on the basis of its possession only by premature abnormal larvae. Its occurrence in the directly developing species *C. obsoleta* and *Glossodoris sibogae* (Usuki, 1967) was considered as evidence for the view that such larval shells are vestigial, pertaining only to capsular development (Hadfield & Switzer-Dunlap, 1984). However, cup-shaped larval shells have been recently reported from planktonic veligers of two lecithotrophic gymnodorid nudibranchs (Boucher, 1986). The still rare occurrence of this type of larval shell and its primitive construction do not preclude its recognition as a valid type.

The variable sculpture and shape of prosobranch larval shells can provide a basis for their identification, but this is not possible with opisthobranch larval shells. Among these, only a few have roughened surfaces and they rarely have characteristic patterns (Hurst, 1967). Colour and exact measurements can nevertheless be reliable characters in certain

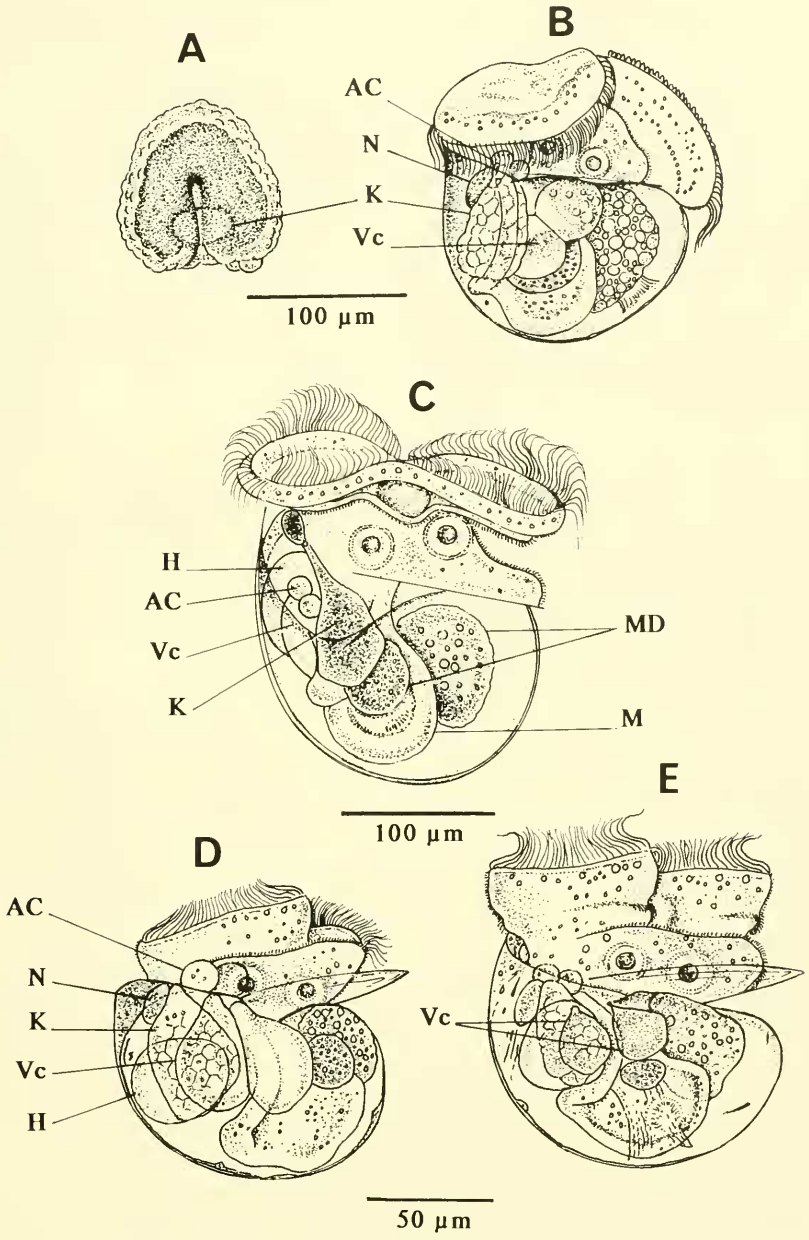


FIG. 4. Embryology and larval development of Red Sea opisthobranchs. A. *Dendrodoris fumata:* early formation of secondary (larval) kidney in gastrula; anal cells in pretorsional position (after Gohar & Soliman, 1967a). B. *Dendrodoris fumata:* 7½ d old embryo. Note excretory structures: nephrocyst, secondary (larval) kidney, and excretory vesicles (after Gohar & Soliman, 1967a). C. *Hexabranchus sanguineus:* newly hatched larva. Note secondary (larval) kidney discharging a large droplet of fluid (modified after Gohar & Soliman, 1963b). D. *Chromodoris inornata:* 7 d old embryo. Note larval kidney and excretory vesicles with attenuated blunt ends (after Gohar & Soliman, 1967b). E. *Chromodoris inornata:* newly hatched veliger with separated excretory vesicles discharging droplets of excretory fluid (after Gohar & Soliman, 1967b). AC, anal cells; H, heart; K, secondary (larval) kidney; M, midgut; MD, midgut diverticula; N, nephrocyst; Vc, excretory vesicle(s).

cases (Gohar & Soliman, 1967g; Soliman, 1978).

As with the early embryological stages, live opisthobranch veligers are ideal material for studying the internal structure of gastropod larvae, e.g. gut, midgut diverticula, retractor muscle, heart, excretory and nervous elements. A heart is said to exist only occasionally in opisthobranch larvae and to have been reported among nudibranchs only for *Adalaria proxima* (Bonar, 1978). In the present material, a pulsatile heart has been described in the nudibranchs *Hexabranchus sanguineus, Dendrodoris fumata, Chromodoris inornata* and *Casella obsoleta* (with 20–21 beats.min-1 in the latter) (Gohar & Soliman, 1963b, 1967a,b,d) (Figs. 4, 5D).

Among the conspicuous larval excretory structures in many nudibranch species are the nephrocysts (symmetrically placed on the anterolateral aspect), the secondary larval kidney, and the large excretory vesicles (located on the right side in the close neighbourhood of the kidney (Fig. 4)). The larval kidney of *H. sanguineus* is highly distinctive by its deep red colour, and clearly has a neck and aperture through which fluid drops are discharged (Fig. 4C). The larval kidney seems to function not only during embryonic and larval life, but also for some time after the juvenile stage is attained (*Casella obsoleta*, Fig. 5D; *Philine denticulata*, Horikoshi, 1967). Very little is known about the excretory vesicles, but the extrusion of hyaline droplets in certain cases (*Chromodoris inornata*, Fig. 4E) suggests they may have an excretory function.

Eyes and tentacles are typical of prosobranch larvae. Their presence in newly hatched opisthobranch planktotrophic veligers is very unusual (Thorson, 1946). They develop 6 days after hatching in *Phyllodesmium xeniae* (pers. obs.), and some time during the larval phase in aplysiids (Switzer-Dunlap & Hadfield, 1977). Some cephalaspids hatch with only the right eye present (*Acteocina canaliculata* (Franz, 1971)), the left eye developing a few days later. Eyes are, however, discernible in the veliger stages of lecithotrophic and directly developing species (*Berthellina citrina, Discodoris erythraeensis* (Gohar & Aboul-Ela, 1957a, 1959), *Trippa spongiosa, Casella obsoleta* (Gohar & Soliman, 1967g,d)) (Fig. 5).

The statocysts develop earlier than the eyes. They are virtually the earliest embryonic nervous elements to develop during gastropod ontogeny and are retained in adult life.

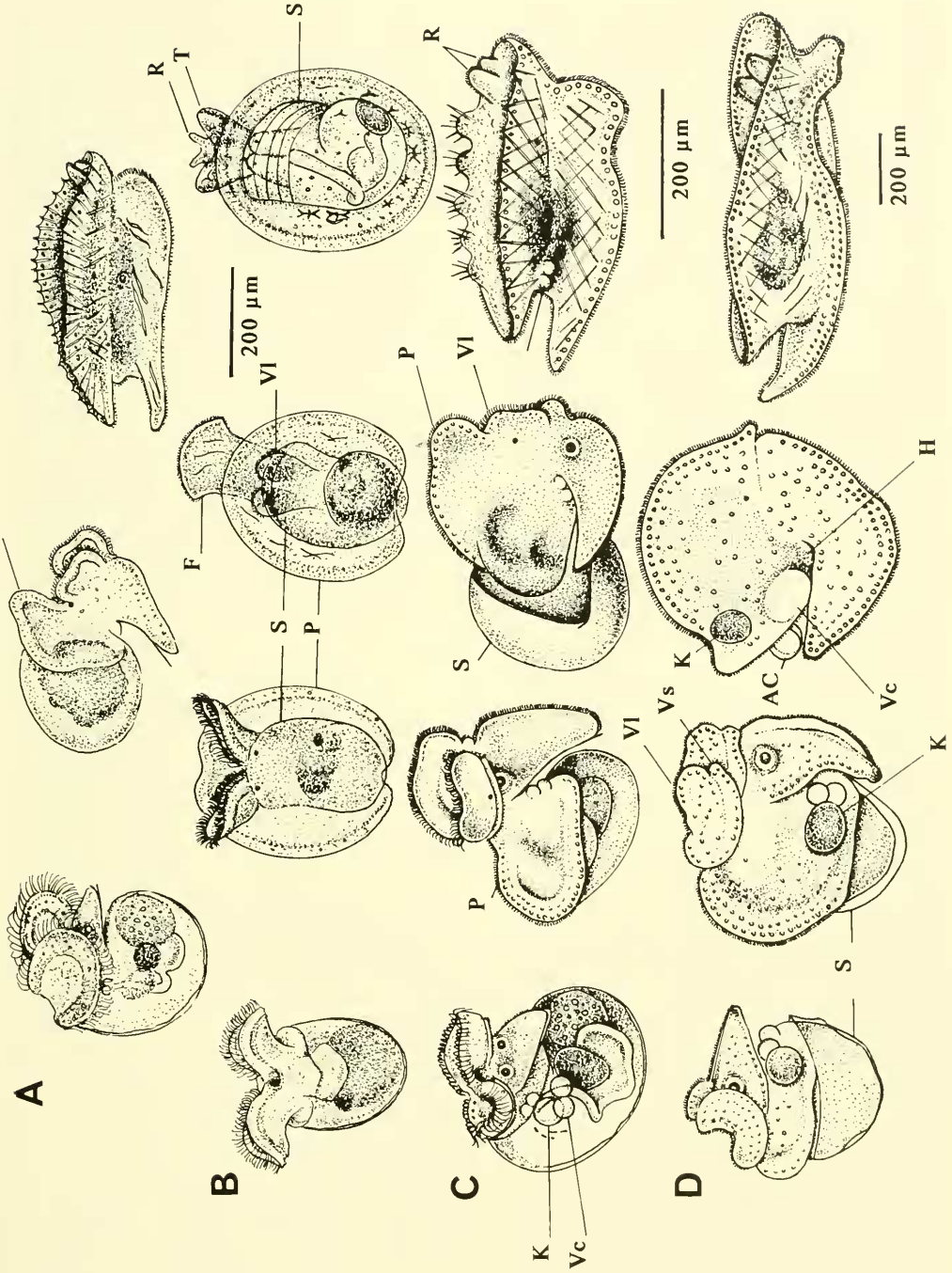
DISCUSSION

Based on the studies of Thorson (1946, 1950), Thompson (1967), Mileikovsky (1971) and Todd (1981) and data of the present study (Table 1), the main types of developmental patterns among gastropods (applicable also to other molluscs) are:

1. Planktotrophic development, with typical veliger larvae feeding during their short or long pelagic existence;
2. Lecithotrophic development, which may be pelagic or non-pelagic; and
3. Direct or capsular development.

Each developmental type is correlated with a specific egg size range. In the present material the egg diameter range for the three types was 60–80 μm, 140–440 μm and 300–330 μm, respectively. This last figure for direct development is, however, based on inadequate data (just a single species, *Casella obsoleta*). Certain factors may, however, intervene allowing relatively small eggs to go through lecithotrophic or direct development, e.g. rich yolk content, rich albumen content of

FIG. 5. Metamorphosis of Red Sea non-planktotrophic opisthobranchs with selected stages of development. A. *Discodoris erythraeensis:* pelagic lecithotrophy in a dorid nudibranch (modified after Gohar & Aboul-Ela, 1959). From left to right: 7 d old embryo; metamorphosing postlarva with reflected mantle fold and no shell; juvenile. B. *Berthellina citrina:* non-pelagic lecithotrophy in a notaspidean (modified after Gohar & Aboul-Ela, 1957a). From left to right: intracapsular veliger stage; newly hatched swimming-crawling stage; pediveliger with absorbed velum and enlarged foot; juvenile with internal shell. C. *Trippa spongiosa:* non-pelagic lecithotrophy in a dorid nudibranch (after Gohar & Soliman, 1967g). From left to right: intracapsular veliger stage; metamorphosing stage; hatching stage deserting its shell; juvenile. D. *Casella obsoleta:* direct development in a dorid nudibranch (after Gohar & Soliman, 1967d). From left to right: intracapsular veliger stage; metamorphosing stage with enlarged foot, subvelar ridge, and reflected mantle fold; embryo, 2 d before hatching, without velum or shell, with anal cells and larval kidney reaching their final detorsional position; juvenile. AC, anal cells; F, foot; H, heart; K, larval kidney; P, reflected mantle fold; R, rhinophore; S, shell; T, tentacle; Vc, excretory vesicle(s); Vl, velum; Vs, subvelum.


A
B
C
D
P
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S
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R
T
200 µm
K
Vc
Vs
AC
H

exceptionally large egg capsules, extracapsular yolk, or presence of nurse cells. Clark & Goetzfried (1978) report even smaller egg diameters of 91.9 μm and 97.7 μm, for the ascoglossans *Elysia papillosa* and *Costasiella lilianae* which develop lecithotrophically and directly, respectively, being provided with extrazygotic food reserves. Extracapsular yolk has been previously described in the spawn ribbons of *Chromodoris tinctoria* (Gohar & Soliman, 1967c). Here, although the egg is 100 μm across, and extracapsular yolk has been shown to be almost depleted before hatching, yet lecithotrophic development was not encountered. Since egg masses were laid in the laboratory only during June and July, animals may proceed to lecithotrophic development at other periods of the year. The development of *Elysia cauze* (Clark & Goetzfried, 1978) is seasonally variable and is apparently controlled by variable utilization of the extracapsular yolk. It is noticeable, however, that in *C. tinctoria,* the newly hatched larvae attained a relatively large size compared with larvae of other species developing from eggs of the same size but having no extrazygotic yolk.

Lecithotrophic development involves a typical veliger stage (which may be the hatching stage) that remains pelagic for a variable period of time, usually not exceeding two weeks (in *Lambis truncata* (Gohar & Eisawy, 1967a) (Fig. 3A); 7 d in *Discodoris erythraeensis* (Gohar & Aboul-Ela, 1959) (Fig. 5A); 4–6 d in *Chicoreus ramosus* (Fig. 3B); 2–3 d in *C. virgineus* (Gohar & Eisawy, 1967b); 2 d in *Strombus tricornis* and 1–2 d in *Fusinus tuberculatus* (Eisawy & Sorial, 1968, 1976a)). During their planktonic existence, which primarily effects their dispersal, the larvae may, but do not necessarily have to, feed. In nonpelagic lecithotrophic development, the veliger stage is passed intracapsularly, and on hatching already metamorphosing swimcrawling or crawling pediveligers are liberated which shortly attain the young stage (*Berthellina citrina, Trippa spongiosa* (Fig. 5B,C); *Cuthona nana* (Rivest, 1978)).

It is not uncommon nevertheless to have pelagic and non-pelagic lecithotrophy occurring in the same species (e.g. *Chicoreus virgineus* (Gohar & Eisawy, 1967b); *Fusinus tuberculatus* (Eisawy & Sorial, 1976a)). In such cases, while the majority of embryos hatch as proper planktonic larvae which start to metamorphose 1–2 d later, a few, having their hatching delayed (possibly due to culture conditions), proceed in development intracapsularly emerging as creeping stages.

In the third type, the whole development and metamorphosis takes place in the embryonic capsule. The veliger stage is either normal, although the velum is not well developed (*Retusa obtusa* (Smith, 1967); *Phyllaplysia taylori* (Bridges, 1975)), or is suppressed to varying degrees (*Casella obsoleta* (Fig. 5D); *Cadlina laevis* (Thompson, 1967)).

Bonar (1978) designates the direct type of development with no proper veliger stage as ametamorphic, exemplified by the dorid *Okadaia elegans* described as having no trace of shell or velum during development (Baba, 1937). This is, however, different from the case of *Casella obsoleta* (included by Bonar among species with ametamorphic development). In this species the veliger stage possesses a reduced but distinct velum, bearing short cilia and a subvelar ridge, and a cup-shaped shell (Fig. 5D). Because metamorphosis does not only affect the locomotory and other external organs, but also (particularly in opisthobranchs) several internal organs including the gut and nervous elements, the use of the term 'ametamorphic' in this context is misleading as it implies that there is no process of metamorphosis. It should appropriately be replaced by 'incomplete' or 'reduced' metamorphosis (i.e. heterometamorphic). Veliger stages with reduced velar lobes, meanwhile, are not restricted to directly developing species, but have also been reported in lecithotrophic species (*Cuthona nana* (Rivest, 1978)) the ontogeny of which could equally be described as involving reduced metamorphosis.

From the above review, the major factors affecting metamorphosis are, in chronological sequence: food conditions, acquiring competence for metamorphosis, and suitable substrata for settlement and metamorphosis. Planktotrophs and pelagic lecithotrophs pass through an obligatory planktonic (precompetent) phase for dispersal and feeding (essential for the former category). Therefore, in laboratory cultures, such larvae should be supplied with suitable food to maintain their survival until after becoming competent to metamorphose. In *Acteocina canaliculata,* only the fed larvae normally metamorphose in culture (Franz, 1971; Mikkelsen & Mikkelsen, 1984). Death of larvae, however, is not only a result of starvation but also of infection by bacteria and ciliates. This has been successfully controlled in laboratories by the use of

selected antibiotics (Bonar & Hadfield, 1974; Hadfield, 1984), ultrafiltration, and/or boiling of sea water before use. Finally, a suitable substratum is essential for metamorphosis in some species. The proximal cue to settlement is probably the presence of specific chemicals which trigger the onset of metamorphosis (Bonar, 1976; Hadfield, 1984), but the advantage of this behaviour is that the settled mollusc has an assured supply of food. Prey organisms of the adult have been frequently reported to be necessary to elicit metamorphosis, while a particular alga must be provided to stimulate settlement and metamorphosis in aplysiids (Switzer-Dunlap & Hadfield, 1977). The specific substratum could also be associated with certain individuals or may provide substances essential for adult life, beside affording optimal conditions for the species. In many species, however, planktotrophic and lecithotrophic larvae, after a period of pelagic existence, normally settle and metamorphose in the absence of a specific substratum (e.g. *Discodoris erythraeensis* (Gohar & Aboul-Ela, 1959); *Acteocina canaliculata* (Franz, 1971); *Pleuroploca trapezium* (Gohar & Eisawy, 1967a), among others).

Other defects in laboratory conditions can possibly also prohibit metamorphosis directly or indirectly. In the present study, rendering the adult's prey or substratum available to the postlarvae of several planktotrophic species (of which many had already become positively geotactic) was unsuccessful in inducing metamorphosis. This involved the use of the definitive coral species bored by the adult in the case of coralliophilids, dead coral pieces for many dorids, the alcyonarian *Sarcophytum* in the case of *Hexabranchus sanguineus* (on which the adults feed, at least in part), and the alcyonarian *Heteroxenia* among whose polyps the aeolid *Phyllodesmium xeniae* lives. Improving laboratory conditions can induce metamorphosis of such larvae developing from large yolked eggs (e.g. *Tonna olearium* (Gohar & Eisawy, 1967a); *Thais savignyi* (Eisawy & Sorial, 1974b)) which otherwise die a few days (6–12) after hatching, and it can help metamorphosing larvae to complete this process successfully (e.g. *Lambis truncata*, whose postlarvae often perish before attaining the young stage (Gohar & Eisawy, 1967a)).

Non-pelagic lecithotrophy and direct development are thus successful modes of molluscan development having advantages over planktotrophy and pelagic lecithotrophy. For the former the dangers of free planktonic existence (e.g. mortality due to predation, starvation, and drifting far from any suitable substratum) are minimized, and no external source of food or a specific substratum for settling and metamorphosing is required. While pelagic lecithotrophic larvae have overcome the food crisis often faced by planktotrophic larvae, they still share with them these other problems. The danger of failing to find a suitable settling ground is even more critical for them than for planktotrophic larvae, because their length of planktonic life is dependent upon their limited yolk supply (Smith, 1967). Non-pelagic lecithotrophs and directly developing species nonetheless have the disadvantages of limited distribution, possible overcrowding and genetic isolation.

The present data agree in general with Thorson's rule (1950) that among benthic invertebrates there is an increase in species with pelagic larvae from the poles towards the tropics and equator. Accordingly, among the 50 species of Red Sea gastropods whose ontogeny has been studied, 35 species (70%) have planktotrophic development, 14 are lecithotrophic and only one (a nudibranch) has direct development. The percentage of pelagic species would appear substantially higher if pelagic lecithotrophic species are taken into consideration. However, within the prosobranchs, the non-planktotrophic species represent a relatively high percentage, i.e. 50% (previously also recorded in the Bahamas (D'Asaro, 1970)), against only 14.3% for opisthobranchs. This may indicate a tendency to planktotrophy among Red Sea opisthobranchs, and to suppress planktonic in favour of non-pelagic development among neogastropods. There are, however, counter views which suggest that ecological conditions in the tropics (Florida, 17–32°C) favour direct development in nudibranchs and Ascoglossa (and probably all opisthobranchs) rather than planktotrophy (Clark & Goetzfried, 1978). While 87% of the nudibranchs studied from our area are planktotrophic, the limited number of species and higher taxa examined do not permit arriving at firm conclusions on this point.

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